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THE STRUCTURE OF THE SPERMATOPHORES OF AMBYSTOMA PUNCTATUM.

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Since the recent paper of Wright and Allen ('09) has again directed attention to the breeding habits of *Ambystoma punctatum*, it has occurred to me that a more careful description of the spermatophores than has yet been given might be of value in a comparative survey of the habits of the urodeles. No adequate figures of these spermatophores have yet been published.

The spermatophores of *Ambystoma punctatum* studied by me at Ann Arbor (Smith, '07) were not freshly deposited, and were not in the best possible structural condition for study; hence only a brief description, illustrated by a photograph, was attempted. Since then I have been able to study these structures in abundance under the best possible conditions. As evidence that the spermatophores were freshly deposited, there may be cited the fact that the spermatozoa of some of them were found to be active when examined in the laboratory seven hours after their collection. The results of this study have confirmed the description previously given by me, in regard to distribution and general structure, but have revealed the common occurrence of compound spermatophores, a condition previously unnoticed.

In the early spring of 1909, when the snow had nearly all disappeared, I found specimens of *Ambystoma punctatum* and *A. jeffersonianum*, under rocks on the hillside near "Branchipus Pond," about two miles from the campus of Syracuse University. The study of the habits of these animals was undertaken in order, if possible, to determine by direct observation the exact procedure in the process of fertilization by means of spermatophores in the case of *A. punctatum*, and to obtain data in regard to *A. jeffersonianum*, in which the manner of fertilization is entirely a matter of conjecture.

Conditions made it impossible to keep a very close watch of the pond during the breeding season, and the abruptness of the weather changes caused me to miss the few opportunities for direct

observation of the activites of the animals in the field, by means of a lantern at night. Specimens of both sexes were transported to the laboratory and kept under observation in aquaria; several males of *A. punctatum*, and one of *A. jeffersonianum*, deposited masses of seminal fluid on the floor of the aquarium, but nothing resembling the formation of true spermatophores occurred. The largest of these masses was nearly 2 cm. long, and the quantity of sperm deposited by each individual was amply sufficient to form a group of spermatophores. The behavior of the sexes toward each other presented nothing that could be interpreted as normal breeding behavior.

In the pond large numbers of spermatophores were deposited, and these were carefully studied, both *in situ* and in the laboratory; but all the specimens collected were identified, with considerable certainty, as the product of *A. punctatum*. The failure to solve the main problems caused me to lay my notes and drawings aside, awaiting an opportunity to continue the investigation; but the conclusive results of Wright and Allen ('09) have made this unnecessary so far as regards *A. punctatum*.

Identification of Species.—The fact that *A. jeffersonianum* occurs, though less abundantly, in the same region with *A. punctatum* made necessary a determination of the species of the spermatophores found. The only available method seemed to be through a study of the spermatozoa. The material available consisted of spermatozoa from a considerable number of individuals of *A. punctatum*, taken both at Syracuse and at Ann Arbor, and spermatozoa from one specimen of *A. jeffersonianum*, taken at Syracuse. Material from each individual was fixed by a variety of methods, stained, mounted and carefully measured under high powers of the microscope. The average measurements were as follows:

	Acrosome	Head.	Middle Piece.	Tail.	Total Length.
A. punctatum	20 μ	116 μ	15.0 μ	480 μ	631.0 μ
A. jeffersonianum	17 μ	114 μ	11.3 μ	348 μ	490.3 μ

It will be seen that the sperm of *A. jeffersonianum* is in general shorter than that of *A. punctatum*. The middle piece is most easily and accurately measured, and affords the readiest means

of differentiating the two species. The range of variation in the length of the middle piece of *A. punctatum* (in several individuals) is 14 μ–16 μ; in *A. jeffersonianum* (in one individual) 11.2 μ–11.9 μ.

The fact that only one individual of *A. jeffersonianum* was considered of course militates against the acceptance of these results as absolutely conclusive; but since material was taken from several individuals of *A. punctatum*, and in all of these there was a decided difference from the results obtained from the single individual of *A. jeffersonianum*, it is highly probable that the species may be distinguished in this way.

Spermatozoa were then taken from a dozen or more spermatophores, each from a different group and presumably deposited by a different individual. This material was treated precisely as in the case of the spermatozoa described above. Somewhat to my surprise and disappointment, all the specimens conformed to the dimensions of the sperm of *A. punctatum*.

Structure of the Spermatophores.—Two general types of spermatophores are recognizable: simple and compound. The compound spermatophores may be roughly divided into the vertically serial, and the Y-shaped types, the former by far the most common; but both these conditions may be found combined in one compound spermatophore.

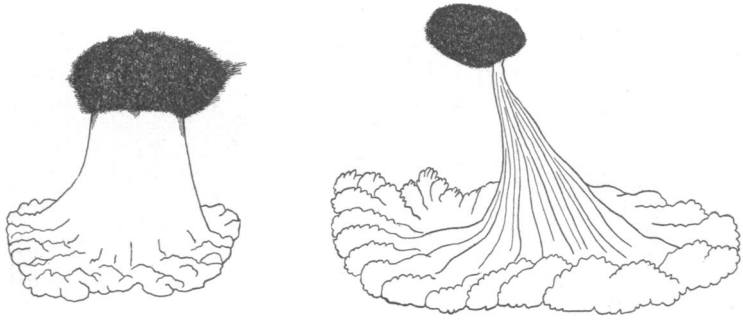
A spermatophore of the simple type is illustrated in Fig. 1. It consists of an expanded hummocky base and a stout stalk, of very clear, transparent, gelatinous material, surmounted by a dome-shaped mass of snowy-white seminal fluid.

While to the naked eye the stalk of a simple spermatophore is perfectly clear, under a low power of the microscope it is seen to possess a delicate network of fibrous material. Under high power this is found to be made up of sparsely distributed spermatozoa, interlaced to form a meshwork. In some spermatophores the strands of this network assume considerable regularity. There may be distinguished regular parallel strands extending in the direction of the axis of the stalk, distributed at about equal intervals through its substance; these strands are connected by more irregular cross-strands.

Evidently a few spermatozoa are present in the cloaca at the

time when the stalk of the spermatophore is laid down, and these spermatozoa owe the regularity of their distribution to the papillated ridges of the cloaca.

For comparison a drawing (Fig. 2) of a spermatophore of *Diëmyctylus viridescens*, obtained from a specimen in captivity, is placed alongside the figure of the simple spermatophore of



1 2

FIG. 1. Camera drawing of simple spermatophore of *Ambystoma punctatum*, × 5. In this and in the following figures the blackened portion is in nature snowy white.

FIG. 2. Camera drawing of a spermatophore of *Diëmyctylus viridescens*, × 5.

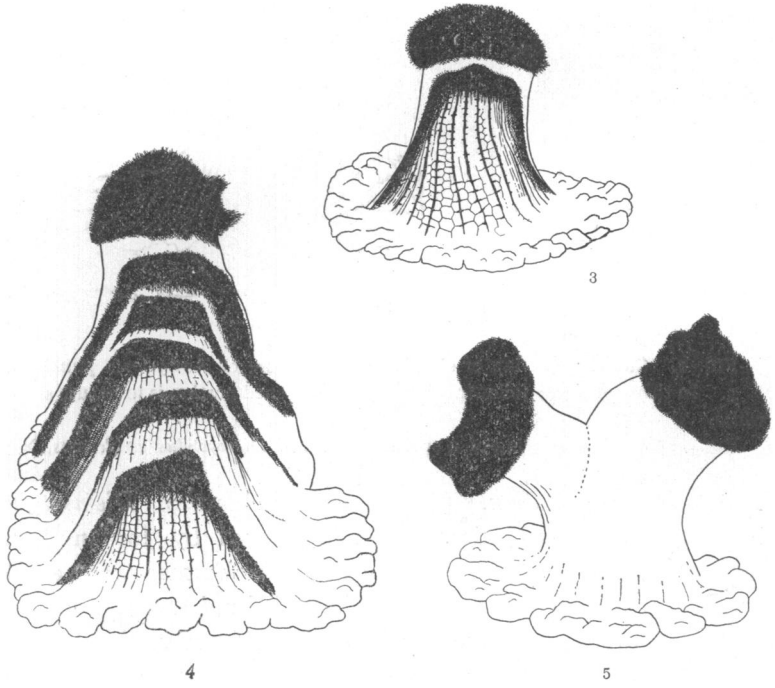
Ambystoma punctatum. (The spermatophore of *Diëmyctylus* has been previously described and figured by Jordan, '93.) Several spermatophores of *Diëmyctylus viridescens* were available for this study, but none of these differed essentially from the one figured. The average dimensions of twelve simple spermatophores of *Ambystoma punctatum* taken at random, and of two uninjured spermatophores of *Diëmyctylus viridescens*, are as follows:

	Total Height.	Longest Diameter of Sperm Mass.	Smallest Diameter of Stalk.	Breadth.
A. punctatum.....	6.2 mm.	3.7 mm.	2.5 mm.	6.4 mm.
D. viridescens.....	8.0 "	2.5 "	0.3 "	12.0 "

The simplest and most common case of compound spermatophore is that in which one spermatophore is deposited directly on top of another (see Fig. 3). In the process of deposition of the second spermatophore the sperm ball of the first one is crushed into the form of an inverted cup covering the stalk of the first, and the sides of this cup are stamped with a characteristic

pattern by the fluted surface of the cloaca. This pattern reminds one of the fainter meshwork seen with the aid of a microscope in the stalk of a simple spermatophore.

By an increase in the number of spermatophores arranged in a vertical series we obtain the extreme form of the serial type shown in Fig. 4, which is made up of six simple spermatophores.



FIGS. 3, 4 and 5. Compound spermatophores of *Ambystoma punctatum*. All the figures are camera drawings, × 5.

FIG. 3. Compound spermatophore consisting of two simple spermatophores, one superimposed on the other.

FIG. 4. Compound spermatophore of the vertical-serial type.

FIG. 5. Simplest case of the Y-shaped type.

Somewhat rarely, compound spermatophores of the Y-shaped type (Fig. 5) are found. These are apparently formed by the deposition of one spermatophore on the side of the stalk of another. In several cases noted, one arm of the Y-shaped stalk was again compound, consisting of two or more spermatophores in series.

Compound spermatophores are not all so regular in form as those figured. Sometimes successive spermatophores are packed together so closely that is it difficult to distinguish individuals in the complex; but while the first impression obtained from some of these spermatophores was that of great irregularity, closer study showed that all of them might be reduced to the vertical-serial type, the Y-shaped type, or a combination of these.

Some of the sperm masses of the simple spermatophores, or the terminal one in the case of a compound spermatophore, were found considerably frayed as if from being taken up into the cloaca of a female; rarely, the entire ball of sperm was missing. It is of course possible that either condition might be accidental.

In one hundred spermatophores taken at random, the number of each kind was as follows:

1. Simple type	23
2. Compound, two in vertical series	45
3. Compound, more than two in vertical series	21
4. Y-shaped, or combination of this type with (2) or (3)	11
Total	100

In none of the spermatophores examined was there any approach to the complexity of structure shown in European urodeles by Zeller ('05). Zeller's drawings appear to me highly conventionalized.

Discussion. — Of the various kinds of spermatophores of *Ambystoma punctatum*, the simple type is functionally the most perfect; yet even this is not so highly differentiated and structurally so well adapted for its purpose as the spermatophore of *Diëmyctylus viridescens*. In case the of *Diëmyctylus*, I have seen almost the entire ball of sperm removed from the very slender stalk by the female cloaca. In *Ambystoma*, on account of the thickness of the stalk affording a large surface for contact with the mass of spermatozoa, this would be more difficult, and according to the observations of Wright and Allen ('09) does not occur — only a very few sperms, comparatively, are detached and retained by the cloaca.

The only mention of compound spermatophores that I find in the literature is in the case of the axolotl, described by Gasco ('81). While in many cases the spermatophores deposited were

single, in one case the male was observed to return repeatedly, at intervals of several minutes, to the same spermatophore and deposit another on top of it, thus building up a compound spermatophore consisting of seven simple spermatophores. Whether the compound spermatophore of *Ambystoma punctatum* is built up in this way I have no means of deciding; it would seem quite as probable that the spermatophores were deposited in rapid succession, while the animal remained in one place — a condition not far removed from what occurs in external fertilization, in which a large amount of seminal fluid is discharged at once. In any case it is difficult to see that any advantage is gained by depositing one spermatophore on top of another and thereby destroying the efficiency of the one previously deposited. As already noted in the case of *Ambystoma punctatum*, the spermatozoa of these spermatophores retain their vitality in water for many hours. The formation of compound spermatophores of the vertical-serial type seems to me a useless and wasteful procedure, and the large proportion of such spermatophores indicates that the spermatophore-forming habit is not highly evolved nor perfectly adapted to its purpose.

In my previous paper (Smith, '07) on the breeding habits of *Ambystoma punctatum*, I ventured the prediction, based on the large number of spermatophores and the manner of their distribution, that the behavior of the adults in the fertilization process would be found to be simpler than in the case of *Diëmyctylus viridescens*. In the latter case only a very few spermatophores are formed by each male, and particular safeguards are necessary in order to insure the delivery of at least one of them to the female cloaca; these safeguards are furnished by the complicated but definite series of acts on the part of the adults which precedes and conditions the deposition of a spermatophore. Just as in the higher vertebrates economy of egg production is correlated with care of the young, so in *Diëmyctylus* economy in the production of spermatophores is accompanied by a considerable amount of certainty as to their fate. This prediction as to the relative simplicity of the behavior of the adults of *Ambystoma punctatum*, the recent observations of Wright and Allen ('09) have abundantly justified. In the light of the observations on

the structure of the spermatophores recorded in the present paper, we can go further and say that the entire process of securing fertilization by means of spermatophores is in *Ambystoma punctatum* more primitive, less highly adapted to secure its object with economy of material, than in *Diëmyctylus viridescens*.

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